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EFFECT OF A POSTPONED MOULT UPON THE SEQUENCE OF PLUMAGE IN CERTAIN PASSERINE BIRDS

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In 1908 I published in the American Naturalist an account of certain experiments on this subject, and since that time I have had so many requests for excerpts that I have thought it advisable to record the experiments again in full in ZOOLOGICA. As this work is to be renewed and elaborated in the future, easy reference to this preliminary paper is desirable.

One of the best-known phases of bird moult is at the commencement of the season of courtship, when the male of many species assumes a more or less brilliant or specialized plumage and in the autumn sheds it in exchange for a more sombre winter garb, often resembling that of the female. In the United States, striking examples are the Scarlet Tanager, *Piranga erythromelas* Vieillot, and the Bobolink, *Dolichonyx oryzivorus* (Linnæus). In Africa, weaver birds of the genera Vidua and Pyromelana, exhibit radical seasonal changes.

The problem which attracted me was the discovery of the factors which determine this seasonal change. So untouched is this field of research that at first no definite method offered itself; there was no previous line of work to be followed or extended. The most hopeful way of work seemed to be to clear the ground by gradually eliminating all negative factors, to demonstrate those conditions which would inhibit such a plumage change, and thus narrow down to the important dynamic phenomena of physiology or external environment. The thousand and one influences which impinge upon the organism from its environment (using that word in its widest sense), may be grouped under certain heads, all or any of which may be concerned in moult and in sexual plumage, change of color

and pattern. These again may operate directly ontogenetically, or indirectly along phylogenetic lines.

Condition of the bird's body—fat or thin.
Food—amount, and whether vegetable or animal.
Blood pressure—raised or lowered.
Sexual organs—active or inactive.
Inheritance.
Temperature—heat or cold.
Meterological conditions of humidity or aridity.

These are only the most apparent factors, they are of unequal value, and some are almost wholly dependent upon others. They represent what I tentatively selected when I first began these experiments, as a convenient review of the general field.

This experiment concerns only the first of the above factors, the condition of fatness or thinness of the bird's body, and its influence on moult. I do not claim that it has further influence than this. The unexpected result in color change or lack of it, must be concerned with influences, other than immediate, acute, physiological conditions.

After all the stress and cares of the breeding season are past, birds such as tanagers and bobolinks are always thin and in poor condition. The worn and bedraggled feathers reflect the actual physical state. The keel of the breast-bone—that true index of a bird's emaciation or obesity—often protrudes conspicuously beneath the skin. Not until the autumn moult is complete do the birds begin to improve and then they may become unusually fat. These general facts doubtless hold good in the case of most birds.

Fat is one of the most insidious dangers incident upon a collection of living birds. Unlike the condition in mammals there is liitle or no external evidence of increasing obesity, and only when the bird is in the hand and the breast feathers blown aside, are the yellow rolls of adipose tissue visible. In the Zoological Park it is necessary to examine many small birds at frequent intervals to ascertain their condition, and to regulate the proportions of the food ingredients accordingly.

In mid-summer I placed several Scarlet Tanagers and Bobolinks under careful observation. None of these birds had been allowed to breed, and so, although it was rather late in the season, they were still in the height of vocal and physical condition. They were all tame, so that, although during the period of experimentation they were confined in rather small cages, each bird in a space of about 12 x 12 x 24 inches, yet their plumage was not damaged by violent struggles caused by fear or a desire to escape, and remained throughout in almost perfect condition.

Little by little I began to cut off the supply of light and slightly to increase the amount of food. This caused a corresponding decrease in activity on the part of the birds, and an almost immediate increase of weight. The great danger from obesity in caged birds is that fright or sudden excitement of any kind, may cause a blood vessel to break, or in some other way bring about death from apoplexy. Consequently I kept the birds in a room where they were never disturbed, and where the absence of noise and other distractions reduced the possibility of an untimely end.

In about a month, when the time for the normal autumn moult arrived, the tanagers and bobolinks were living the "simple life" in a dim illumination, and although consuming a fair amount of food, were exercising but little. The time for the autumn moult came and passed and not a single feather was shed. The cages were made intentionally of wire mosquito netting, the fine mesh of which would have caught and revealed any feathers had any been moulted. In addition to this, the birds were examined twice a week, and nowhere on body or head was there any evidence of moulted, or of new, incoming feathers. On blowing away the breast feathers the yellow sub-cutaneous layer of fat could be seen, which in a bird caged under normal conditions, would have been a danger symptom not to be disregarded.

As the winter gradually passed, it was evident that the birds had skipped the autumn moult entirely, and appeared to suffer no inconvenience as a result. As far as appearance went they were in perfect health, showing only the symptoms of

inactivity consequent upon an excess of adipose tissue. Early in the experiment the songs of the birds became less frequent and sustained, and finally died away altogether, and when a good layer of fat had accumulated, seldom was even a chirp uttered.

From time to time a bird was brought gradually into a brighter light and meal-worms added to its diet. This invariably resulted in a full resumption of song. Even in the middle of winter a tanager or a bobolink, would, under these conditions make a room ring with its spring notes, and with this was correlated a slight decrease in weight. This phase of the experiment could not be prolonged indefinitely, however, for the song period seemed limited, just as it would be under normal conditions even in non-breeding birds, although the nuptial plumage remained unchanged throughout the winter. As one of my keepers pithily put it, "We have their calendar twisted backward."

A sudden alteration in temperature—either higher or lower —wrought, I found, a radical change in the physical metabolism of the birds. Under such conditions, they would cease feeding almost altogether, and one tanager lost weight rapidly. A few feathers on the neck fell out and in the course of about two weeks this individual moulted every feather and came strongly into his normal winter plumage of olive green. The metabolism set up by the change in temperature, in its extent and rapidity seemed comparable only to the growth of a deer's antlers.

Early in the following spring individual tanagers and bobolinks were gradually brought under normal conditions and into their seasonal activities, with quick result. Just as the wild birds in their winter haunts in South America were at the same time shedding their winter garb and assuming the more brilliant hues of summer, so the birds under my observation also moulted into the colors appropriate to the season. Herein lay the significant fact of the whole experiment: *The old scarlet and black feathers fell from the tanagers and were replaced by others of the same color*; *and from buff, cream and black, the bobolinks moulted into buff, cream and black!* There was no exception;

the moult was from nuptial to nuptial, not from nuptial to winter plumage. The dull colors of the winter season had been completely suppressed.

We thus have proof that the outward manifestation of the sequence of plumage in these birds is not in any way predestined through inheritance bringing about an unchangeable succession, in the case of the tanager, of scarlet-green, scarlet-green, year after year. The katabolic changes of pigmentation in the blood are induced by certain seasonal factors, whether internal, as the sexual organs, or external, as food or changing meteorological conditions, we know not. But we do know that this orderly succession may be interrupted by certain external conditions in the environmental complex.

The pigmental changes in the blood which induce the green autumn garb, undoubtedly went on as usual in my birds. The one individual which reacted to the change in temperature proved this. But in course of time, although this pigment was not permitted to be expended in its normal feather-impregnation, it was changed by some seasonal alchemy, and the scarlet pigment made ready. When at last I permitted the moult to take place, the bird was clothed in the dress appropriate to the season, and if wild, would have suffered no handicap in the functions for which its brilliance is intended. It is interesting to note that the green plumage which was so completely suppressed, is unquestionably the more ancestral and primitive, as it is the garb of the young of both sexes and of the adult female.

Nature offers us a curious comparison and normal control in the Summer Tanager, *Piranga rubra* (Linnæus), the male of which retains the scarlet plumage throughout the year. So that what I was able to induce by abnormal methods, is the normal sequence in this closely, indeed generically, related species.

Until I have further and more complete data, checked by results derived from control of other factors of the environment, I shall refrain from further comment on the significance of this initial experiment.

There is genuine satisfaction in thus making even the merest beginning at the elucidation of these problems, which in

their general evolutionary aspect are of far wider application than to the class *Aves* alone. And work along these lines is all the more enjoyable because success demands the continual life and good health of the individual birds upon which the experiments are carried out.